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Grazing and aridity reduce perennial grass abundance in semi-arid rangelands – Insights from a trait-based dynamic vegetation model

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ABSTRACT

Semi-arid tropical rangelands substantially contribute to livelihoods of subsistence farmers, but are threatened by undesired vegetation shifts due to climate change and overgrazing. Grazing-induced shifts of the grass community composition are often associated with rangeland degradation. To identify sustainable management strategies, a process-based understanding of grass functional diversity and rangeland dynamics is required. We present a new scheme for aDGVM2, a dynamic vegetation model for tropical ecosystems, that distinguishes annual and perennial grasses based on trait trade-offs to improve the representation of rangeland communities. Additionally, the model includes a new scheme that describes selective grazing and grazing effects on grass-layer composition. We tested the new model version for various grazing intensities along a precipitation gradient in South Africa. Mean annual precipitation below 500 mm constrained rangeland productivity and carrying capacity. Increasing grazing intensity reduced rangeland productivity and increased annual grass abundance. Heavy grazing resulted in annual grass dominance. Livestock preferred perennial over annual grasses at low grazing intensities at all except the two driest sites; preference switched to annual grasses at intermediate intensities, and became non-discriminating at high grazing intensities. Rangeland recovery after removal of grazers required 2–15 years. We conclude that management intervention reducing or eliminating grazing pressure during and after stress years is crucial to allow rangeland recovery and avoid permanent degradation.

1. Introduction

Grazing is an important ecosystem process with respect to the area affected globally and the amount of plant biomass converted into animal biomass (Huntly, 1991). Rangeland grazing also provides a substantial contribution to the livelihoods of people who depend on subsistence farming (Herrero and Thornton, 2013). In semi-arid rangelands, grazers and grasses share a co-evolutionary history, and grazing has been identified as one of the key determinants of semi-arid grasslands, aside from water availability and fire (Walker, 1987). However, intensive grazing combined with climate change may negatively affect ecosystem services provided by rangelands and thereby threaten livelihoods of (subsistence) farmers (Adeel et al., 2005; Guuroh et al., 2018). Intensive grazing can trigger vegetation changes that may promote as well as deter further grazing (Hempson et al., 2014), because grazing selectively removes biomass based on its palatability. This modifies the species composition of herbaceous communities, changes distribution and frequency of traits, and alters the prevalence of functional types (Díaz et al., 2007; Linstädter et al., 2014; Moreno Garcia et al., 2014). For example, shifts in perennial-to-annual grass ratio can result from (over-)grazing alone, but may be aggravated by additional global-change agents such as drought (O'Connor and Roux, 1995; O'Connor, 1995; Reynolds et al., 2007; Ruppert et al., 2015), with substantial negative consequences for dry-season feed availability, rangeland carrying capacity, and local livelihoods (Martin et al., 2016). In particular the loss of perennial species affects productivity, quality, and duration of forage availability, and can lead to desertification where transition to bare-ground conditions is involved

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(Schlesinger et al., 1990; Ruppert et al., 2015; Guuroh et al., 2018). Whether (over-)grazed rangelands can recover from the associated adverse effects is a highly relevant question for rangeland managers coping with rangeland rehabilitation. Resting may in some cases allow recovery of forage quantities, but not necessarily of forage quality and palatability (Seymour et al., 2010), whereas severely degraded rangelands may not even recover after several decades of resting (O'Connor, 1991; Müller et al., 2007).

It is challenging to predict the responses of rangelands to changing grazing regimes due to the complex interactions between grazers, vegetation, and climate. A process-based system understanding is needed to develop sustainable land-use strategies for rangelands, in particular under altered future climate conditions (Müller et al., 2015). Although field studies from semi-arid tropical rangelands reveal differential effects of grazing on plant communities (Kohyani et al., 2008; Linstädter et al., 2014), the results of local studies depend on site-specific environmental conditions and a site's evolutionary and land-use history. Contradictory observations make it difficult to extrapolate grazing impacts on vegetation from site-scale to larger scales. In this context, models are useful tools. They are simplified representations of reality that allow to conduct simulation experiments on interactions between grazing, climate change, and fire and to test a wide range of alternative management options on large spatio-temporal scales.

Dynamic global vegetation models (DGVMs) can simulate how vegetation interacts with environmental forcing factors, e.g., climate, CO_2, and disturbances. DGVMs help to assess effects of environmental change on vegetation patterns and biogeochemical cycles (Cramer et al., 2001; Chang et al., 2017). To support large-scale spatio-temporal applicability many DGVMs use a restricted number of plant functional types (PFTs, Lavorel et al., 2007). This approach successfully captures responses of biogeochemical cycles and broad vegetation patterns (Cramer et al., 2001). However, while PFT-based DGVMs distinguish approximately 5–8 woody PFTs (e.g., Hickler et al., 2012), they only differentiate between C_3 and C_4 grass types. C_3 and C_4 grasses in many DGVMs are largely spatially exclusive due to bioclimatic constraints that limit their spatial occurrence (e.g., minimum coldest-month survival temperature of C_4 grasses and maximum-coldest-month temperature for establishment of C_3 grasses at 15.5 °C in LPJ and LPJ-GUESS, Sitch et al., 2003; Smith et al., 2001). Hence, PFT-based DGVMs de facto represent grasses by one single PFT at the local scale, although in reality both grass types do co-occur (Sage et al., 1999; Lattanzi, 2010). While coarse-scale shifts in the competitive balance of woody and herbaceous plant types can be captured based on such a simple grass representation (Higgins and Scheiter, 2012), within-grass-community dynamics remains invisible. In rangelands, where grasses predominate and provide the main forage source for grazers, such a representation is highly inadequate. In order to study functioning and biodiversity, to assess rangeland sensitivity to grazing, to test management scenarios, and to deduce sustainable management and conservation strategies, a more refined representation of grasses in DGVMs is necessary (Linstädter et al., 2014; Bond, 2016).

We argue that DGVMs should at least distinguish annual and perennial grasses to reflect the 'principal dichotomy' between two very different life-history strategies in semi-arid rangelands (Smith and McAllister, 2008). While smaller-scale rangeland models have included distinctions between annual and perennial grasses in combination with selective grazing for more than a decade (e.g., Liedloff et al., 2001; Lohmann et al., 2012), DGVMs so far widely ignore within-grass-layer diversity. DGVMs that are capable to distinguish functional differences between annual and perennial grasses will allow a more realistic representation of spatio-temporal patterns of forage provision in semi-arid tropical rangelands.

Leaf and growth traits of annual and perennial grasses affect their respective sensitivity to grazing, as well as productivity, seasonal availability and forage quality, i.e., palatability, and thereby grazing selectivity (e.g., Pontes et al., 2007). However, not only do grass traits influence grazer choices, but grazers' selectivity in return also exerts selection pressure on grasses (Augustine and McNaughton, 1998). Grazing selectivity therefore is an important driver of perennial–annual grass abundance. Nonetheless, only a few DGVMs include grazing routines (e.g., Chang et al., 2013; Pachzelt et al., 2015; Scheiter and Savadogo, 2016; Rolinski et al., 2018), and none of them a representation of grazing selectivity or differentiation of trait diversity within the grass layer. Using aDGVM2, a DGVM for tropical ecosystems (Scheiter et al., 2013; Langan et al., 2017), we developed a new grass scheme to model annual and perennial grasses and a grazing routine that simulates selective grazing. The latter is indispensable for modeling grazing impacts on annual-perennial community dynamics, as grazing can shift the balance of annual and perennial grasses and lead to decrease in perennial grass abundance (e.g., Dyksterhuis, 1949; Olsvik-Whittaker et al., 1993; Tessema et al., 2011). We use the updated version of aDGVM2 to test the sensitivity of semi-arid rangelands to varying grazing intensities for five sites located along a precipitation gradient in South Africa. We ask the following questions:

1 Is annual precipitation a determinant of rangeland productivity, and does the maximum density of livestock supported by semi-arid rangeland ecosystems increase with increasing mean annual precipitation?
2 Does increasing grazing intensity lead to shifts in the community composition of rangelands due to selective grazing?
3 Can continuous intense grazing without intermittent resting periods prevent recovery and can it keep rangeland communities in a state of low productivity and forage quality?
4 Is recovery of rangeland communities from intense grazing mediated by mean annual precipitation, i.e., does mean annual precipitation (MAP) influence post-disturbance regrowth?

Based on our results, we discuss implications for sustainable grazing management of semi-arid rangeland ecosystems.

2. Methods

2.1. Model description

The aDGVM2 simulates growth of individual plants on a representative stand of 1 ha and tracks their state variables. Each plant individual is characterized by a set of traits describing plant type (grass or tree, perennial or annual), leaf characteristics (specific leaf area, photosynthetic pathway), carbon allocation to plant compartments, plant architecture (roots and crown shape), response to fire, reproduction and mortality. Growth, reproduction and mortality of plants are the combined result of trait characteristics and environmental conditions. Plant performance is regulated by trait trade-offs (mass conservation for allocation, stability trade-offs for architecture, leaf economic spectrum, and resource competition between individuals, see Scheiter et al., 2013; Langan et al., 2017, and references therein). Trait inheritance and alteration during reproduction affect community assembly and allow dynamic adaptation to environmental conditions. For more details, see the aDGVM2 model description in Scheiter et al. (2013) and Langan et al. (2017). In aDGVM2, the simulated representative 1ha vegetation stand is subdivided into equal-sized subcells (thereafter denoted as patch) containing maximum one type of individual at a given time, thereby limiting the maximum number of individuals simulated for each stand. The prescribed sub-grid structure also allows to track neighborhood relationships between individuals, e.g., to determine competition for light and space. Patches can be occupied, bare, become bare, and be re-colonized by a new individual with potentially different traits following mortality of the original individual. In sensitivity tests conducted prior to this study with individual numbers ranging between 25 × 25 and 60 × 60 individuals, 40 × 40 individuals had proven sufficiently numerous to represent the full range of trait diversity, while keeping computational effort

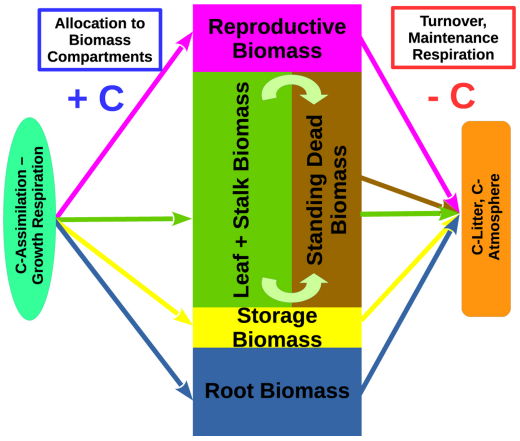

Fig. 1. Carbon allocation, carbon-fluxes and biomass pools of an individual grass patch in aDGVM2. Standing dead leaves and stalks contribute to within-patch self-shading before they are gradually transferred to the surface litter pool.

reasonable. As single grass individuals in the model are constrained to a maximum cover of $1\,m^2$, their respective mass- or area-based state variables are multiplied by patch area size to obtain a patch's value. This implies trait homogeneity within a patch. Fig. 1 illustrates carbon balance and biomass pools of an individual grass patch.

Here we present a novel scheme for aDGVM2 that distinguishes between annual and perennial grass types, and a grazing scheme that allows to simulate selective grazing based on status and traits of individual grass patches. Due to the trait- and individual-based representation of plants in aDGVM2, we are in a unique position that allows us to implement a distinction of grass functional types based on trait trade-offs. To our knowledge, this is the first time such a detailed representation of grass traits and selective grazing has been implemented in a DGVM, and it addresses the issue that the relevance of grasses is often neglected in classical PFT-based DGVMs that often focus mainly on diversity and dynamics of woody vegetation.

2.2. Implementation of annual and perennial grasses

We conceptualized annual and perennial grasses by assigning different trait ranges for carbon allocation, specific leaf area (*SLA*, $[m^2\,kg^{-1}]$), and seed size vs. seed number, based on empirically observed trade-off costs between allocation to reproductive vs. vegetative structures (Friedman and Ruin, 2015). For a conceptual overview, see Table 1. Annual grasses feature rapid production of photosynthetic leaf biomass and quick reproduction as they need to complete their life cycle within one growing season. Higher allocation to reproductive structures at the expense of investment to vegetative structures in annuals has been described by various authors (e.g., Hancock and Pritts, 1987; Vico et al., 2016), although such trade-offs can be masked by variability in resource availability and fitness of individuals (van Noordwijk and de Jong, 1986). Selection for rapid gain of leaf area at the beginning of the growing season in annuals is accomplished at the cost of leaf thickness, entailing higher *SLA* values (Garnier, 1992; Poorter et al., 2009), lower capacity to extract soil water, and lower leaf longevity (Langan et al., 2017, and references therein). Allocation trait ranges for annual and perennial grasses in this version of aDGVM2 are listed in Table 2. Trait parameters of plant individuals are randomly assigned during initialization from a functional type's respective allowed trait range, are inherited by offspring, and are subject to mutation and crossover during reproduction (Scheiter et al., 2013). Allocation parameters are scaled such that their sum equals 1.

Table 1
Implementation of annual and perennial life strategies for grasses in aDGVM2. Allocation trade-off between reproductive and vegetative structures is based on Friedman and Ruin (2015).

Annuals	Perennials
Differences in allocation	
Higher allocation to leaves and seeds	Higher allocation to roots and storage
Lower allocation to roots and storage	Lower allocation to leaves and seeds
Differences in phenology	
Active for only one growing season	Gradual biomass die-back during drought/low light; regrowth from reserves at start of growing season
Differences in mortality	
Phenology-based mortality	Negative C-balance
Death after one growing season	Background mortality
	Grazing-related mortality

Table 2
Parameter ranges for carbon allocation traits (fraction of total assimilated carbon) of annual and perennial grasses, and the default parameters used for grasses in the original version of aDGVM2. Allocation traits are scaled to sum to 1.

Parameter	Description	Annuals	Perennials	Default
A_l	Allocation to leaves and stalks	[0.4;0.8]	[0.25;0.4]	[0.25;0.5]
A_{re}	Allocation to reproduction	[0.3;0.5]	[0.05;0.3]	[0.05;0.2]
A_{ro}	Allocation to roots	[0.2;0.4]	[0.4;0.8]	[0.2;0.8]
A_s	Allocation to storage	[0.0;0.2]	[0.2;0.4]	[0;0.4]
A_{S2L}	Re-allocation storage to leaves	[0;0.7]	[0;0.7]	[0;0.7]

Perennial plants switch between a dormant (respiratory) and a metabolic (assimilatory) state once light or water availability exceed or fall below plant-specific phenology thresholds. These threshold values determine the onset and end of leaf growth of perennials in the growing season. Seed germination of all grasses is also tied to leaf phenology, i.e., crossing the leaf phenology thresholds also triggers seed germination and initiates seedling growth at growing season start. To operationalize differences in recruitment, annuals in the model have a higher germination likelihood than perennials. This assumption is required because the number of individuals modeled on a simulated vegetation stand is limited, and new individuals can only establish on non-occupied patches. As only one randomly chosen seed per empty spot is allowed to germinate at a time, the germination likelihood serves to reflect differences in seed density and ensures that annuals can persist in the population.

Perennials experience gradual biomass die-back during drought or low-light conditions, while annuals die at the end of the growing season when water or light availability drop below an individual's phenology thresholds. Annual and perennial grasses in their assimilatory state experience leaf turnover, with leaf longevity being inversely related to *SLA* (Langan et al., 2017). Mortality of perennial grasses may be related to age (background mortality), grazing stress (see Section 2.3), or negative annual carbon balance. A negative C-balance can be caused by insufficient C-gain (e.g., due to water stress, competition, self-shading), or too high C-loss due to respiration, turnover, fire, or grazing (see, e.g., Zimmermann et al., 2010).

2.3. Grazing model

Previous versions of aDGVM2 did not include grazing routines (Scheiter et al., 2013; Langan et al., 2017). In this updated version of aDGVM2, we simulate selective grazing by linking grass removal to state variables and trait values of individual grass patches. To our knowledge, this is the first time such an approach has been implemented in a DGVM. A schematic overview of the grazing scheme is provided in Fig. 2.

Daily biomass demand, B_g $[kg\,day^{-1}]$, is defined by requirement per

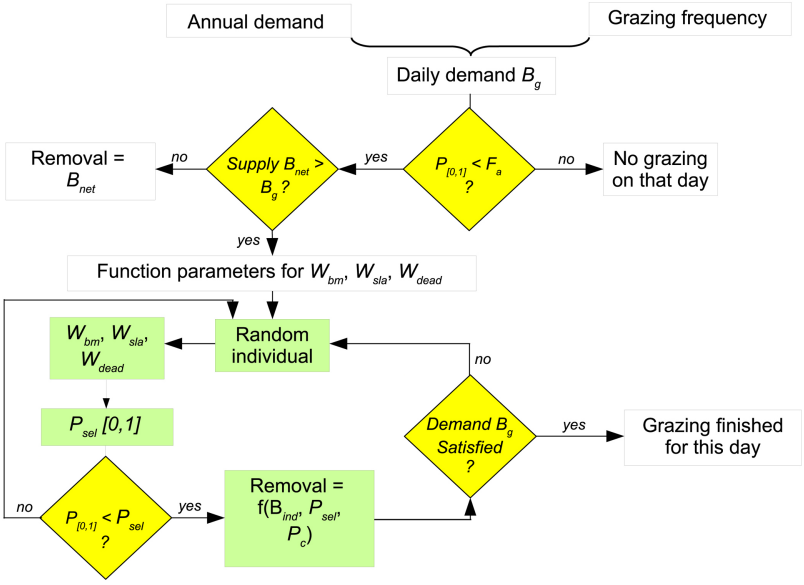

Fig. 2. Flowchart illustrating the grazing scheme implemented in aDGVM2. Abbreviations: B_g: daily biomass demand per LU [kg day^{-1}]; P[0, 1]: random uniform number between 0 and 1; P_c: random uniform number between 0 and 0.1; F_a: grazing frequency; B_{net}: net biomass available for grazing [kg]; W_{bm}: biomass weighting factor; W_{SLA}: *SLA* weighting factor; W_{dead}: moribund material weighting factor; P_{sel}: combined selection likelihood, averaged across W_{bm}, W_{SLA} and W_{dead}; B_{avail}: grazer-available aboveground grass patch biomass [kg].

Table 3
List of state variables used in the grazing model.

Variable	Variable description	Variable unit
ANPP	Aboveground primary productivity	[kg]
B_{avail}	Grazer-available aboveground grass patch biomass	[kg]
B_g	Daily biomass demand per LU	[kg day^{-1}]
B_{net}	Maximum consumable aboveground grass biomass	[kg]
$B_{realloc}$	Biomass reallocated from storage reserves to leaves	[kg]
$B_{removed}$	Biomass removed from individual grass patch	[kg]
B_{stor}	Biomass of storage compartment	[kg]
C_c	Biomass consumed from grass patch within one year	[kg year^{-1}]
C_f	Fraction of ANPP consumed by grazers	[–]
d_g	Number of days per year a grass patch experienced grazing	[days]
F_a	Grazer presence, fraction of days per year	[–]
F_{loss}	Living biomass removed from patch by grazing, as fraction of total	[–]
I_a	Factor derived from d_g	[days]
M_g	Grazing-related probability of mortality	[–]
N_a	Number of grazing animals	[ha^{-1} day^{-1}]
NPP	Annual total net primary productivity (aboveground + belowground)	[kg]
P_c	random number between 0 and 0.1	[–]
P_{sel}	selection likelihood, between 0 and 1	[–]
SLA	specific leaf area	[m^2 kg^{-1}]
W_{bm}	biomass-derived weighting factor, between 0 and 1	[–]
W_{dead}	dead-to-living-biomass-derived weighting factor, between 0 and 1	[–]
W_{SLA}	*SLA*-derived weighting factor, between 0 and 1	[–]

livestock unit (LU), multiplied by animal number (N_a, [animals ha^{-1} day^{-1}]; see Table 3 for overview of state variables). Grazers remove leaves and stalks, reproductive biomass and standing senescent and moribund grass material (compare Fig. 1). To account for the lower nutritional value of dead biomass, we assign it 2/3 of the nutritional value of living plant material (estimate based on Fig. 4 in Bell (2006)). In this study, we treat grazing as an external forcing controlled by the number of LU per day and hectare, N_a, and the visitation frequency F_a (fraction of days per year during which grazers are present). We refrain from simulating grazer population dynamics and focus on managed land where stocking rates are controlled by land owners as we are interested in how varying grazing pressure affects grass communities, and not how biomass supply feeds back on the livestock population. Negative balance between demand and supply is tracked, but its implications for grazers are ignored for the purpose of this study, implicitly assuming that grazers move through the landscape to compensate for their deficit elsewhere, or that farmers will provide supplementary feed if required (Müller et al., 2015).

When B_g exceeds stand-level biomass, aboveground grass biomass B_{net} is removed down to stubble irrespective of grass type (retaining 0.01 kg leaf/stalk biomass and reproductive biomass per plant, respectively), i.e., all grass patches are grazed irrespective of selection probability. Belowground plant biomass is indirectly affected by grazing via carbon balance effects. Roots may experience die-back after leaf loss because low carbon assimilation leads to reduced carbon allocation to roots, causing root maintenance respiration to exceed C-allocation.

If supply B_{net} exceeds B_g, biomass is selectively removed from grass patches until B_g is satisfied. In an iterative cycle, grass patches are randomly targeted for grazing, and if the drawing of a second random number for a targeted grass patch is less than that patch's selection probability P_{sel}, grass biomass is removed from that patch. The selection probability P_{sel} determines (i) the likelihood of a specific grass patch to be grazed, and (ii) the fraction of grass biomass removed from a grazed patch. P_{sel} is based on leaf biomass, fraction of living-to-dead leaf material, and *SLA* as a palatability proxy (Kelvin et al., 2010), as these are state variables and traits readily available in aDGVM2. Using the range of available biomass and *SLA* of all grass patches on a representative stand, we calculate three separate selection probability values for each grass patch and combine the biomass-derived (W_{bm}), *SLA*-derived (W_{SLA}), and dead-to-living-ratio derived (W_{dead}) probability value to the overall selection probability P_{sel}. To determine the three probability values, for each probability a linear equation is fit between the two individuals with the highest and lowest respective value (biomass, *SLA*, dead-to-living-ratio) in the population, assigning a weight of 1 to the individual with the highest and a weight of 0 to the individual with the lowest value. Grass individuals with less than the minimum biomass required for grazing are ignored (selection probability of 0). Each grass individual's respective probabilities are then determined using the derived linear equations for biomass, *SLA*, and dead-to-living ratio. P_{sel} is calculated as the mean of W_{bm}, W_{SLA} and W_{dead}, and describes the overall likelihood that an individual grass patch is grazed. This likelihood is high if patch biomass and palatability are high. Large proportions of dead biomass decrease P_{sel}, as dead biomass conceals living biomass in tufts. Avoidance of tufts with greater amounts of moribund material has been observed in field studies (e.g., O'Connor, 1992). The amount of biomass cropped from a patch is based on its aboveground biomass and P_{sel}, in average removing larger relative amounts of biomass from patches with larger P_{sel}. Biomass removal $B_{removed}$ (in [kg]) is

Table 4
Study sites, sorted by mean annual precipitation (MAP). MAP and elevation were obtained from New et al. (2002).

Site label	Coordinates	MAP (mm)	Elev. (m)	Site information
S1	30.969° S, 22.128° E	253	1317	Carnarvon Experimental Farm, Nama Karoo Biome, sheep grazing experiments (van den Berg and Du Toit, 2014; Du Toit et al., 1995)
S2	27.750° S, 23.083° E	419	1223	Savanna Biome (Linstädter et al., 2014; Oomen et al., 2016)
S3	29.417° S, 26.750° E	591	1471	Grassland Biome (Linstädter et al., 2014; Oomen et al., 2016)
S4	23.850° S, 29.683° E	607	1318	University of Limpopo, Syferkuil Experimental Farm, Savanna Biome, DroughtAct Experiment (grazing and artificial drought, http://www.ag-linstaedter.botanik.uni-koeln.de/drought_act.html)
S5	22.879° S, 30.482° E	826	845	Thohoyandou, University of Venda, Savanna Biome

calculated as a function of an individual's available biomass B_{avail} (in [kg]) and its selection probability P_{sel}:

$$B_{\text{removed}} = B_{\text{avail}} \cdot P_{\text{sel}} + (B_{\text{avail}} - B_{\text{avail}} \cdot P_{\text{sel}}) \cdot P_c \quad (1)$$

with P_c as a random number between 0 and 0.1 adding bite imprecision to the removal based on P_{sel}. Biomass is removed in equal proportions from living leaf biomass, dead leaf biomass, and reproductive biomass, but limited to the respective maximum available amount. We set a minimum removal per biomass pool (minimum bite size) of 0.01 kg as long as the respective pool has sufficient biomass, in order to avoid removal of very small quantities and associated large numbers of iteration cycles to cover daily demand. In principle, a grass patch can be grazed several times during 1 day. However, as a grazed patch's P_{sel} is updated based on its new lower biomass, the likelihood to be re-selected on the same day decreases.

Both annual and perennial grass patches partially replace lost leaf biomass on a daily basis by reallocating carbon from storage compartments (growth compensation, see, e.g., McNaughton (1983), Ferraro and Oesterheld (2002)). The amount of carbon reallocated from storage to leaves ($B_{realloc}$, in [kg]), is determined by the fractional loss of original leaf biomass, F_{loss}, and the individual grass patch's trait value defining the maximum allowed transfer fraction from storage (B_{stor}, in [kg]) to leaves, A_{S2L}:

$$B_{\text{realloc}} = F_{\text{loss}} \cdot B_{\text{stor}} \cdot A_{S2L}, \quad (2)$$

with fraction A_{S2L} being a life-history trait.

Grazing may increase plant mortality through negative annual C-balance. As post-grazing recovery can be boosted via reallocation from storage to new leaf tissue, plant mortality is also influenced by the size of the storage compartment, the allocation-to-storage trait A_s, and the storage-to-leaf reallocation trait A_{S2L} (Table 2). We additionally calculate a grazing-stress factor between 0 and 1 that defines the likelihood of plant death from grazing stress. This stress factor depends on how many times an individual patch was grazed within one year, and the fraction of annual *ANPP* (aboveground net primary productivity, in [kg]) that got consumed. This approach accounts for empirical evidence that recovery duration has a major impact, with longer time for recovery from defoliation and more time between defoliation events significantly decreasing negative effects (Ferraro and Oesterheld, 2002). Short recovery intervals may be more detrimental than a singular high-intensity grazing event, as infrequent high-intensity grazing has been reported to disrupt the carbohydrate metabolism of perennial plants less severely (Menke, 1992). In aDGVM2, grazing-related mortality probability depends on the number of days a specific grass patch had to endure grazing and on how severely it got impacted, measured by the fraction of *ANPP* that got consumed over the course of a year. Each perennial patch's annual grazing mortality probability, M_g, is calculated as

$$M_g = I_a \cdot C_f^2, \quad (3)$$

where I_a is a factor related to the number of days per year d_g a specific individual was grazed, and the consumed fraction C_f is the fraction of annual *ANPP* eaten by grazers.

$$I_a = \frac{0.9}{364} \cdot d_g + \frac{35.5}{364}, \quad (4)$$

This equation assumes that for a C_f of 1 (worst-case scenario) the mortality risk based on the number of grazing days equals 10% after one grazing event and linearly increases to 100% if vegetation is grazed daily. C_f is the fraction of annual *NPP* allocated to leaves and reproduction that got consumed by grazers:

$$C_f = \frac{1}{A_l + A_{\text{re}}} \cdot \frac{C_c}{\text{NPP}}. \quad (5)$$

Here, *NPP* (in [kg]) is annual net productivity (aboveground and belowground), C_c (in [kg year $^{-1}$]) is the amount of biomass consumed from one individual patch over the course of the year, A_l is the fraction of *NPP* allocated to leaves, and A_{rep} is the fraction of *NPP* allocated to reproduction.

2.4. Simulation experiments

We conducted control simulations without grazing for five study sites along a precipitation gradient in South Africa's semi-arid rangelands (Table 4, Fig. 3a). The sites were chosen to connect to past and ongoing field research performed at these locations. Where available, we compare our simulated results with site-specific data from rangeland experiments, or ground data from semi-arid rangelands with comparable environmental conditions. For more details on site-specific details and references to field-research conducted at the sites, see Table 4. To ensure that model state variables and trait assemblies stabilize, we let the model equilibrate to ambient environmental forcing for 500 years (spin-up), then simulated another 200 years without grazing using iterated monthly data from the CRU reference climatology for the period 1961–1990 (New et al., 2002). We generated daily rainfall sequences from the climatology by using the algorithm provided by New et al. (2002). Test simulations showed that approx. 400–500 simulation years are sufficient to reach dynamic equilibrium of model state variables. Per site, we conducted 10 replicate simulation runs with different initializations of the plant community to account for stochastic effects in precipitation and community assembly. Each replicate run was initialized with its respective unique and reproducible random seed, i.e., variability between replicate runs was ultimately caused by the differing random seed.

For the grazing experiments, we simulated 100 years of continuous grazing after the spin-up phase, followed by another 100 years without grazing to allow recovery. Per site, we conducted simulations with 10 different grazing intensities (biomass demand B_g of 5, 10, 15, …, 50 kg ha^{-1} day^{-1}), at a default grazing frequency of 0.2, i.e., animals are present for approx. 20% of the days per year. Note that unique random seeds for replicate runs between different treatment scenarios were the same, e.g., run No. 1 was always initialized with the same random seed in all scenarios. Therefore, differences between scenarios with the same unique random seed are solely due to differences in treatment.

As we were specifically interested in our novel distinction between annual and perennial grasses and how the relative abundances of these

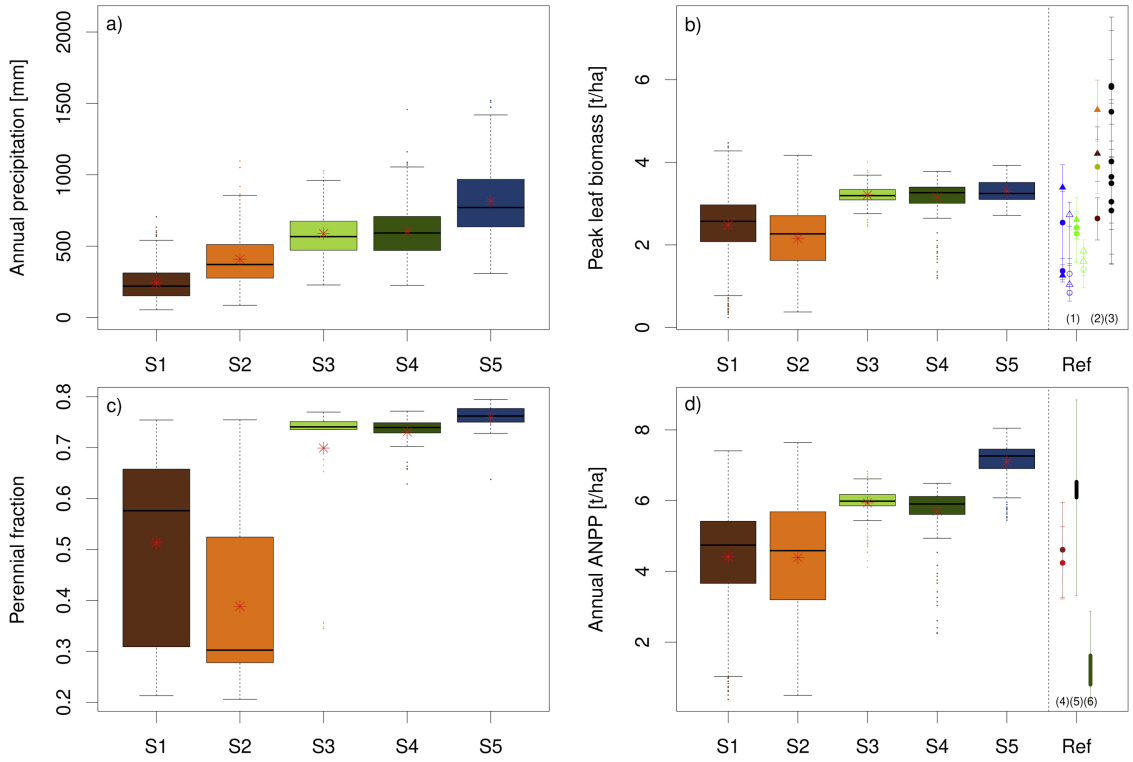

Fig. 3. (a) Site-specific simulated annual precipitation; (b) annual peak-leaf biomass; reference values are from: (1) Oomen et al. (2016), Fig. 2; blue symbols: grassland; green symbols: savanna; circles: spring data; triangles: autumn data; filled symbols: commercial land; open symbols: communal land; values are median values, ranges extend from 1st to 3rd quartile; (2) Moustakas et al. (2013), Fig. 1, grass biomass at 200% tree canopy radius distance, site mean values and standard deviations; (3) Dwyer (2011), Table 1, column 3, site mean values and standard deviation; (c) fraction of perennial grasses in the stand-level population. (d) Stand-level annual aboveground primary productivity (*ANPP*); reference values are from: (4) Knapp et al. (2006); (5) Scurlock et al. (2002), Table 4, Nairobi grassland mean values and standard deviations; (6) DroughtAct data from Syferkuil for years 2015–2017 (unpublished), range of mean values of experimental plots, and minimum and maximum value across all plots and years. Boxes for simulated data indicate first and third quartiles, whiskers extend to 1.5 times the interquartile range, red asterisks indicate mean values. All data are from the 20-year period of the control scenario corresponding to the last 20 years of grazing in the grazing simulations (simulation years 581–600).

herbaceous PFTs were modulated by climate and selective grazing, we deliberately excluded fire and woody vegetation, although they are part of aDGVM2 (Langan et al., 2017). This simplification is justified because tree cover at the study sites is low and large areas of these rangelands are grass-dominated. This experimental design allows us to focus on the grass layer and the interactions between different grass types, grazing, and environmental drivers and avoids the common focus on woody vegetation types in DGVMs.

3. Results

3.1. Ungrazed communities

Simulated living grass biomass was subject to large intra- and interannual variability. Fig. 3b illustrates the simulated range of annual peak-leaf biomass for the control scenarios. Peak-leaf biomass on average reached 2–2.5 t ha^{-1} at the two driest sites S1 and S2, and 3–3.5 t ha^{-1} at the wetter sites S3 to S5. Sites S1 and S2 displayed higher interannual variability than the wetter sites. Annual stand-level *ANPP* (Fig. 3d) varied between ca. 4–5 t ha^{-1} at the two driest sites and ca. 6–7 t ha^{-1} at the wetter sites. At the two driest sites *ANPP* showed high interannual variability. Without grazing, perennial grasses dominated the sward at the three wetter sites (Fig. 3c). The two dry sites had lower median values of perennial grass abundance (30% and 58%, respectively) and high temporal variability in the ratio between perennial and annual grasses.

Annual precipitation was a weak predictor of annual *ANPP*. Tests for correlation and cross-correlation between *ANPP* and precipitation revealed low correlation factors (see also scatterplots in supplementary Fig. S1). However, productivity tended to be correlated to productivity of preceding years (for details on autocorrelation of *ANPP*, see supplementary Fig. S2). This dependency was stronger at the more productive sites due to lower interannual fluctuations in productivity. Our results from the baseline control simulations therefore only partially confirm the first part of our first key question. MAP below 500 mm constrained simulated peak-leaf biomass and *ANPP*, while above 500 mm, precipitation became less relevant as a limiting factor, as further precipitation increase did not reflect in peak-leaf biomass and only to some degree in *ANPP* (Fig. 3). Variability in peak-leaf biomass and annual *ANPP* was markedly higher for the two dry sites S1 and S2 than for the three wetter sites although variability in annual precipitation was comparable for all sites. This higher variability of *ANPP* is due to the large interannual variability in perennial fraction at S1 and S2 caused by drought-induced die-back of perennials, i.e., years with low perennial abundance are also marked by low peak-leaf biomass and productivity. At sites S3–S5, annual precipitation is sufficient to sustain a stable population of perennials in most years, resulting in less variability of peak leaf biomass and *ANPP*.

3.2. Effect of grazing on productivity and community composition

Increasing grazing intensity reduced *ANPP* (Fig. 4a), with the amount of *ANPP* for a given grazing intensity depending on the initial productivity of the site. The wettest site S5 displayed the highest average annual productivity when undisturbed, and at low to intermediate grazing intensities reduction in productivity was

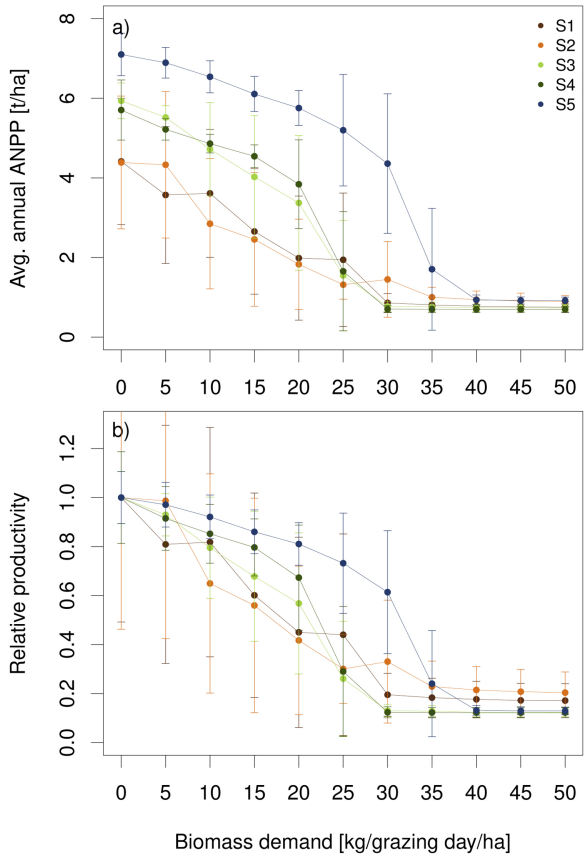

Fig. 4. (a) Effect of grazing intensity on average *ANPP*, averaged across all replicates for the last 20 years of the simulated grazing period; (b) decline in *ANPP* relative to ungrazed control. Error bars indicate standard deviation across replicates and 20-year-period.

approximately linear in absolute (Fig. 4a) as well as relative (Fig. 4b) terms. The approximately linear decrease in productivity with increasing grazing intensity became nonlinear, i.e., productivity started to drop more steeply, once demand started to exhaust supply.

Increasing biomass demand could be sustained until annual aboveground productivity became insufficient to fully compensate removal (Fig. 5). Sites S4 and S5 had the highest carrying capacities; site S5 sustained a continuous long-term demand of 25 kg ha^{-1} grazing day^{-1}, while at site S4 a grazing intensity between

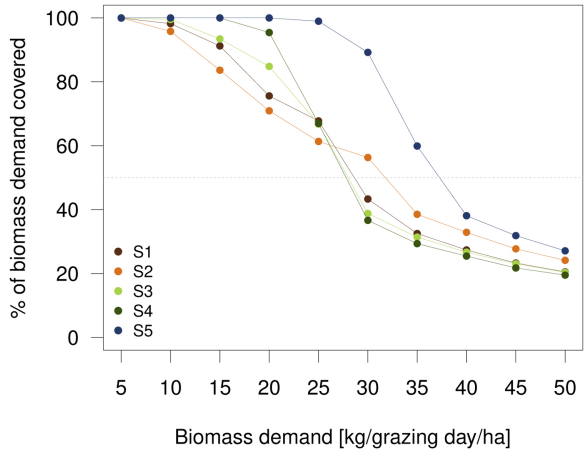

Fig. 5. Comparison between available biomass and biomass required by grazers, calculated across all replicates for the full 100-year duration of the simulated grazing experiment, for sites S1–S5.

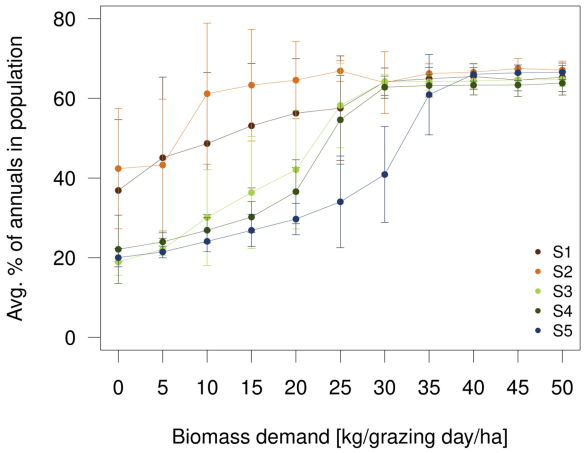

Fig. 6. Effect of grazing intensity on relative abundance of annual grasses in the simulated stand-level population, averaged across replicates for the last 20 years of the grazing period. Error bars indicate standard deviation across replicates and 20-year-period.

15 and 20 kg ha^{-1} grazing day^{-1} could be sustained in most years. Long-term carrying capacity tended to increase with MAP, with lowest carrying capacity at the two driest sites. With respect to the second part of our first key question, we can say that average carrying capacity of rangelands increases with MAP.

The proportion of annual grasses in the population increased with grazing pressure (Fig. 6). Without grazing, the average percentage of annual grasses varied between 20 and 40%, with more annuals at drier sites. As long as demand could be satisfied, increase of annual grasses with intensity was moderate, but increased steeply at the expense of perennial grass abundance once the site productivity became insufficient to cover grazing demand (compare Fig. 5 and 6). Without grazing, annual grasses contributed less than 10% to *ANPP* at all study sites due to low abundance and their short life span. With increasing grazing pressure, plot-level *ANPP* declined (Fig. 4), perennials became less abundant (Fig. 6), and productivity was increasingly provided by annual grasses, with as much as 70–80% contribution at the maximum grazing intensity simulated in this study. Regarding our second key question, our results confirm that grazing as a selective process may affect community composition, and thereby alter rangeland productivity and quality.

As described in Section 2, an individual grass patch's likelihood to be grazed is influenced by its *SLA*, its aboveground living biomass, and its ratio of living and dead biomass. Annual grasses typically reached lower peak-leaf biomass than perennials due to their ephemerality and the thinner leaves resulting from their higher *SLA*, a selection mechanism that enables them to quickly increase leaf area at low biomass investment. Hence, at low grazing intensities grazers mostly grazed perennial grasses as their higher biomass outweighed their lower *SLA*. Fig. 7 illustrates how the average likelihood of being grazed for both annuals and perennials varied between sites and grazing intensities. Avoidance vs. preference of annuals in Fig. 7 was determined by relating the fraction of grazings per year on annuals to their fraction within the grass population, i.e., a value of 1 indicates that annuals were grazed as often as can be expected based on their occurrence in the population, whereas a value greater/less than 1 indicates that annuals were grazed more/less frequently than can be expected based on their occurrence. A value of 2 indicates that annuals were grazed two times more frequently than can be expected based on their occurrence. The amount of biomass withdrawn from perennials vs. annuals also changes with grazing intensity (see Fig. S3), with annuals becoming the dominant biomass source at high grazing intensities.

At the lowest grazing intensity (5 kg ha^{-1} grazing day^{-1}), preference of perennial over annual grass patches was common except for

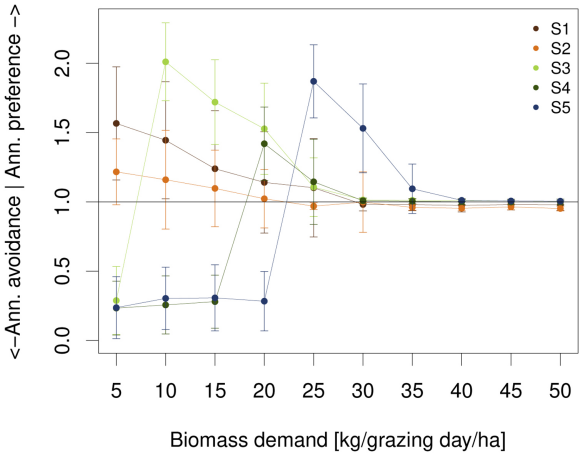

Fig. 7. Grazer selection of annual vs. perennial grasses as a function of grazing intensity, averaged across all replicates for the last 20 years of the grazing period. A value of 1 signifies no preference, values between 1 and 0 indicate increasing discrimination against annual grasses, while values between 1 and 2 indicate preference of annual grasses. Error bars indicate standard deviation across replicates and 20-year-period.

the two driest sites S1 and S2. This effect was particularly pronounced for sites S4 and S5, the sites that had high peak-leaf biomass and *ANPP* as well as low annual abundance in the control scenario. However, the drier, less productive sites S1 and S2 were characterized by animals preferentially grazing annual grasses or no discrimination against annuals or perennials.

As grazing intensity increased, preference at sites S3–S5 switched from perennials to annuals. However, when grazing intensity approached carrying capacity, discrimination gradually decreased. At high intensities, annuals and perennials were grazed without discrimination. Discrimination tended to be highest at the more productive, wetter sites, at low to intermediate grazing intensities. At more arid, less productive sites discrimination was less pronounced. Discrimination decreased as resources became increasingly scarce, because at high grazing intensity all available individuals on a representative stand had to be grazed to (at least partially) meet demand.

3.3. Supply transgression and post-grazing recovery

The biomass demand that ultimately exceeded supply differed between sites (Fig. 4) and replicate runs for one site (Fig. 8). A combination of temporal variability of productivity, variability of annual rainfall, and dynamic balance between increasing grazing intensity and concurrent decrease in productivity influenced if and after how many years supply started to exceed demand. For example, at site S4 a demand of 15 kg ha^{-1} grazing day^{-1} could be covered over the entire 100-year period in all ten replicate runs, but a demand of 20 kg ha^{-1} grazing day^{-1} was only met in nine replicate runs. During one run, demand exceeded productivity after approx. 40 years of continuous grazing. For a demand of 25 kg ha^{-1} grazing day^{-1}, only 30% of replicate runs maintained sufficient productivity to continuously cover demand for 100 years. A grazing intensity of 30 kg ha^{-1} grazing day^{-1} exhausted carrying capacity after a maximum of 20 years in all replicate runs. Qualitatively, the tipping point with respect to grazing intensity at site S4 is therefore reached approximately at a demand of 25 kg ha^{-1} grazing day^{-1}, as variability between replicate runs is largest for this level of demand. Once carrying capacity had been exceeded, pre-collapse productivity was never recovered while grazing persisted. In accordance with our third key question, our results indicate that continuous intensive grazing may prevent recovery and keep rangelands in a less productive state.

However, productivity and community composition recovered after grazing stopped. Recovery duration depended on preceding grazing intensity and potential site productivity. With respect to our fourth key question, we identified an indirect relation between MAP and recovery time, with the more productive sites taking longer to recover their full productivity potential, which is due to the higher biomass and *ANPP* that needs to be regained at the wetter sites. In our simulations 5–10 years were usually sufficient to regain 90% of the productivity level of the ungrazed control (Fig. 9) for any grazing intensity at the two dry sites, and for grazing intensities of less than 20 kg ha^{-1} grazing day^{-1} at the wetter sites. The average population ratio between annual and perennial grasses and stand-level peak-leaf biomass also recovered to the level of the ungrazed control scenario following the temporal pattern of productivity recovery (figure not shown).

4. Discussion

While rangeland ecologists often use sophisticated classification schemes to characterize grass species' palatability and responses to grazing (Dyksterhuis, 1949; van Oudtshoorn, 1999), these classification approaches are not easily transferable to rangelands with a different community composition and/or climatic setting (Linstädter et al., 2014) and are thus not feasible for DGVMs. We present a novel scheme for aDGVM2 that conceptualizes distinctive traits and resulting differences in life-history strategies of perennial and annual grasses. We focus on the community assembly of the grass layer and its dynamics because grazing not only affects the competitive balance between woody and herbaceous vegetation, but also alters composition, productivity and palatability of the grass layer. As a selective process, grazing feeds back on forage quality and carrying capacity and causes vegetation changes that can promote or deter further grazing (Hempson et al., 2014). We are aware that we are not considering the full range of criteria defining palatability. *SLA* is a simplified surrogate for palatability, and not all herbivore species base their dietary selection equally on *SLA*. Moreover, *SLA*–palatability relationships may vary considerably across African grasslands (Ferner et al., 2015). However, additional palatability-related factors such as leaf tensile strength, leaf nitrogen content, overall nutritional value, concentration of defensive leaf phenolics and structural compounds, or toxicity currently cannot be deduced from plant traits simulated by aDGVM2. Nonetheless, based on the definition of a few generalized selection criteria, we are able to model effects of grazing selectivity that are in agreement with empirical observations, such as the shift to higher annual grass abundance at expense of perennial grasses.

Our simulated peak-leaf biomass of 2–3.5 t ha^{-1} in ungrazed rangeland communities is within the typical range reported for semi-arid African rangelands (Dwyer, 2011; Moustakas et al., 2013; Oomen et al., 2016). *ANPP* values reported for semi-arid tropical rangelands are less certain and vary over a wide range depending on location, site-specific conditions, and method used to estimate *ANPP* (Scurlock et al., 2002). Knapp et al. (2006) report an average of 4.24 ± 1.02 t ha^{-1} for the grassland trials at Ukulinga research farm in Kwazulu-Natal, South Africa, while *ANPP* values between 3.31 and 8.85 t ha^{-1} with a mean of 6.09–6.53 t ha^{-1} have been reported for rangeland near Nairobi (Scurlock et al., 2002). For neotropical rangelands, Ospina et al. (2012) measured *ANPP* values between 8.98 and 15.6 t ha^{-1}. Average *ANPP* estimates from the DroughtAct grazing experiments performed between 2015 and 2017 at Syferkuil experimental farm near University of Limpopo, in South Africa's Limpopo Province, range between 0.8 and 1.62 t ha^{-1} for perennial grasses in grazing exclusion plots (minimum 0.21–0.47 t ha^{-1}, maximum 0.123–2.87 t ha^{-1}, E. Mudongo, J.C. Ruppert and A. Linstädter, unpublished data). Simulated *ANPP* values are therefore within the range reported for semi-arid rangelands, but higher than the values estimated in the DroughtAct grazing experiments. Yet, these experiments include exceptionally dry years experienced in Southern Africa due to the 2015/2016 El Niño, one of the strongest of the last 145 years (Winkler et al., 2017). Simulated peak-

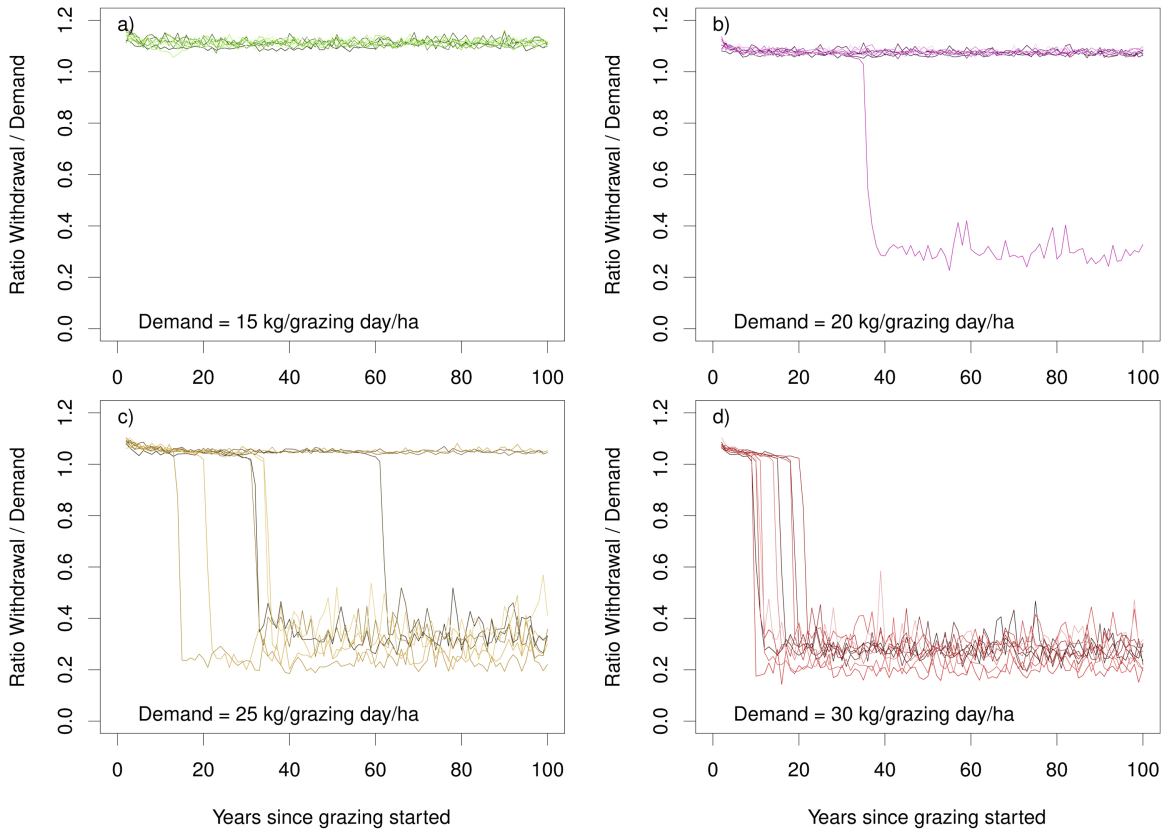

Fig. 8. Ratio between biomass withdrawal and demand for site S4, on a yearly basis, for increasing grazing intensity. Lines represent replicate runs. As long as demand can be satisfied, the ratio of withdrawal to demand may exceed 1 because daily step-wise biomass removal from individuals stops once the sum of biomass removed from different grass patches exceeds B_g for the first time.

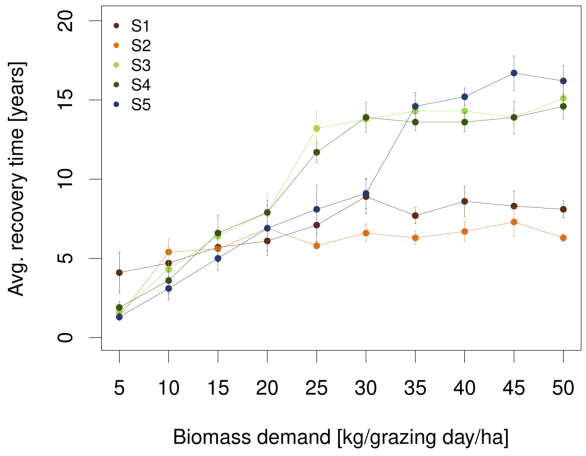

Fig. 9. Years required to recover 90% of the 100-year mean productivity of the control scenario. Bars indicate standard error of mean across replicates.

leaf biomass and *ANPP* varied between sites, with lower values and a wide range of interannual variability at the two driest sites, where perennial grasses reach the limit of their ecological niche. While wetter years still provide sufficient precipitation to sustain perennial grass cover at these sites, dry years cause substantial die-back of perennial grasses, lowering peak-leaf biomass and shifting community composition towards more ephemeral annual grasses.

Intensive grazing as well as low MAP reduced productivity and promoted annuals. This finding agrees with grazing-induced changes observed in semi-arid tropical rangeland systems (Walker et al., 1981; Linstädter et al., 2014). Replacement of perennials by annuals has been interpreted as a shift in the competitive balance in favor of short-lived, disturbance-adapted annuals (Dyksterhuis, 1949). After weak disturbance, persisting perennial grasses quickly expand cover at the beginning of the subsequent growing season. More intense disturbances increase mortality of perennials in aDGVM2, leading to more open space in the simulated vegetation stand that becomes available for new plant seedlings. As annuals need to establish each year, they benefit from a high overall mortality and open space created by perennial turnover.

Shifts towards annual dominance decreased biomass supply for grazers, as annuals provided less biomass and productivity per grass patch than perennials. This agrees with studies reporting lower leaf area and biomass produced per unit rain for annuals than perennials (Nicholson et al., 1990; Beck et al., 1990). There are several possible reasons that could explain this pattern. First, annuals germinate, build up biomass, reproduce and die within one growing season. In comparison, perennials gradually die back during the dry season, but storage reserves help to quickly rebuild biomass in the next growing season. Second, after germination simulated perennials often required several growing seasons to reach maximum values of peak-leaf biomass, time that annuals intrinsically lack. Third, simulated annual grasses had thinner leaves and higher *SLA*, enabling them to quickly gain leaf area after establishment, but resulting in overall less leaf biomass. This deficit is additionally amplified by proportionally higher carbon allocation to reproduction. Continental-scale applications of grazing models, e.g., Pachzelt et al. (2015), identified net primary productivity and dry-season length as good predictors of grazer density. However, by ignoring grazing-induced community shifts, these models may overestimate productivity under high grazing intensity. Heavily grazed communities were more akin to those of drier sites, i.e., intensive grazing and drought had similar effects on simulated grass communities. These results agree with the convergence model of aridity and

grazing postulated for grass-dominated ecosystems and supported empirically, e.g., by Quiroga et al. (2010), Linstädter et al. (2014) and Gaitán et al. (2018).

Simulated overgrazing effects carried over to subsequent years and sites did not recover without resting (Fig. 8). This supports recommendations (e.g., Müller et al., 2015) to adjust grazing management during post-drought years to avoid permanent productivity loss and undesired community shifts. Grazers' preference for young, tender leaves can prevent regrowth and promote less palatable and/or less productive plants (O'Connor, 1995). After grazing suppression, our sites recovered productivity within 5–15 years (Fig. 9). This agrees with observations from field studies, e.g., O'Connor (1995) reports more rapid recovery for sites with a low-intensity grazing history. In the worst cases, vegetation has been observed to remain in a degraded state for at least 20 years after exclusion of large herbivores (Walker et al., 1981). Persistent heavy grazing may also delay recovery by depleting local seed banks (O'Connor, 1991, 1992; Sternberg et al., 2003). Moreover, recovery of perennial grasses in arid and semi-arid rangelands may also depend on the occurrence of a "window of opportunity of regeneration", such as several years with high rainfall (see Linstädter et al., 2014, and references therein). Recovery may also be impeded if overgrazing causes soil loss due to increased erosion, altered balance of soil nutrient cycles, or altered soil water availability due to increased run-off. We may therefore overestimate rangeland recovery potential due to the simplified nature of our experimental design and soil degradation mechanisms currently not represented in the model. In addition, competitive interactions between grasses, woody vegetation, grazing and fire may cause permanent shifts in vegetation structure, a set of interactions that we acknowledge, but that lies beyond the intended scope of this study.

Our results have implications for sustainable management of semi-arid rangelands. Grazing can reduce drought resistance of rangelands and amplify drought effects, in particular negatively affecting perennial grasses (Vetter, 2009; Ruppert et al., 2015). Management should aim to avoid the loss of perennials from populations and seed banks due to drought-stress and/or overgrazing (Danckwerts and Stuart-Hill, 1988) as perennials provide feed more reliably than the ephemeral annuals. Downsizing of herds and/or provisioning of supplementary fodder should include post-stress years when recovery of reserve and green biomass is stimulated, providing time to regain levels sufficient to buffer precipitation deficits and grazing losses (Danckwerts and Stuart-Hill, 1988; Müller et al., 2007). As we could demonstrate, once productivity has collapsed it often remains depressed without sufficient resting (compare, e.g., Danckwerts and Stuart-Hill, 1988). Contrary to the needs of subsistence farmers who usually aim for maximum stocking density rather than maximum sustainable yield, resting promotes improvement of rangeland conditions and allows higher total stocking rates within a certain period of time (Müller et al., 2007).

5. Conclusions

We developed a grass scheme for aDGVM2 that allows us to functionally differentiate annuals and perennials. This enables us to model within-grass-layer dynamics and grazing effects on grass community composition. Our results corroborate empirical evidence that climate and grazing interactively alter community composition of semi-arid grass communities (Linstädter et al., 2014). We find that drought and intensive grazing have similar effects on perennial/annual ratios in semi-arid grass-dominated ecosystems, as both shift community composition towards higher abundance of annuals. Concomitant declines in productivity reduce grazing carrying capacity and entail lower carbon storage. Therefore, DGMVs omitting within-grass-layer dynamics may misjudge the carbon balance of semi-arid rangelands, grazing impacts and rangeland carrying capacity under future conditions. Our results also corroborate the need for flexible, informed management of semi-arid African rangelands found by previous studies to prevent overgrazing from locking grass communities in undesired low-productivity states. Modeling grasses as individuals with dynamic traits and defining characteristic trait-based functional differences between annuals and perennials is a promising step towards a long-needed improvement of grass representation in DGVMs. Further refinement of grass representation in aDGVM2 could include additional grass-related traits, e.g., distinction between increaser and decreaser types, or the capability for non-sexual reproduction and spread via stolons. Moreover, we are confident that the new grass layer dynamics and grazing scheme presented in this study are a necessary basis that will allow evaluation of more complex interactions between grasses, grazing, fire, shrub encroachment, nutrient dynamics and anthropogenic management interventions in savanna ecosystems.

Authors' contributions

MP developed the grass scheme and grazing routine presented in this study, performed the simulations and analyzed the results. SS, LL and SH developed the version of aDGVM2 that served as basis for this current version. SS, LL, SH, CM and CG contributed to further development of aDGVM2 and helped brainstorming ideas during development of the new grazing routine and grass scheme. MP and SS led the writing of the manuscript. AL, JR and EM provided conceptual and empirical information on the ecology of savanna grasses and semi-arid rangelands as well as access to unpublished data from the LLL DroughtAct grazing experiments at Syferkuil Experimental Farm. All authors contributed substantially to the improvement of manuscript drafts.

Data accessibility

Selected data are available at http://data.sasscal.org/metadata/view.php?view=li_rbis_process_step&id=6386. To obtain the model code please contact the authors.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2018.12.013.

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